

# DIVERSITY AND BIOSTRATIGRAPHY OF THE DIPROTODONTOIDEA OF RIVERSLEIGH, NORTHWESTERN QUEENSLAND

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The diversity and distribution of Riversleigh's Diprotodontoida is discussed with respect to current understanding of the local stratigraphic sequence. The more plesiomorphic diprotodontid and palorchestid taxa are restricted to the older System A Local Faunas. *Neohelos* and *Propalorchestes* range throughout Systems A, B and C exhibiting a morphocline. Stage-of-evolution biocorrelation with other Australian and New Guinean Tertiary mammal faunas is in accord with previously established biostratigraphic hypotheses. However some basal Riversleigh deposits may predate the central Australian Wipajiri and Etadunna Formations. Diprotodontoid diversity is high in System A deposits, low in System B and relatively high in System C. Abundance is high in System C deposits and low in Systems A and B. Only two taxa extend into the Pleistocene. Patterns of diversity and abundance are discussed in view of Australia's changing Cainozoic climate. □*Diprotodontidae*, *Palorchestidae*, *Riversleigh*, *Tertiary*.

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The paucity of radiometrically dated Australian Tertiary freshwater fossil deposits has resulted in marsupial stage-of-evolution biochronology being the most commonly employed method of dating fossil assemblages (Woodburne et al., 1985). Fundamental to this method is an adequate understanding of phyletic succession within the taxon (Megirian, 1994). Chronologic and phyletic succession within diprotodontoid lineages are well documented (e.g. Stirton et al., 1967; Murray, 1990b; Murray et al., 1993). Consequently, the group has played a major role in previous biochronologic analyses (e.g. Stirton et al., 1967; Woodburne et al., 1985; Woodburne et al., 1993; Archer et al., 1994; Archer et al., 1995) and has contributed significantly to the construction of the chronological framework of Australia's Tertiary mammal faunas.

Similarly, because of limited stratigraphic data and the lack of radiometric dates, much of the current chronologic sequence of Riversleigh's local faunas has been constructed on the basis of vertebrate biocorrelation (Archer et al., 1989). Recent reappraisal of diprotodontoid material from Riversleigh indicates at least 9 genera and 18 species. This paper outlines the diversity and distribution of diprotodontoids throughout the Riversleigh Systems and discusses their bearing on current biostratigraphic understanding. Biocorrelation of Riversleigh's Oligocene-Miocene deposits with other Australian fossil assemblages is also discussed.

Lithostratigraphy and Systems terminology follow Archer et al. (1989, 1994a). Cusp nomenclature follows Archer (1984) and Rich et al. (1978). Molar homology is that proposed by Luckett (1993). Premolar number follows Flower (1867). Higher level systematic nomenclature follows Aplin & Archer (1987).

## BIOSTRATIGRAPHY

Figure 1 lists the diprotodontids and palorchestids from different local faunas within Riversleigh's stratigraphic units. These units are defined by Archer et al. (1989, 1994a): System A, late Oligocene to early Miocene; System B, early to middle Miocene; System C, middle to early late Miocene; and Pleistocene assemblages.

*Silvabestius michaelhirti* is the most plesiomorphic zygomaticine recognised (with the possible exception of *Raemotherium yatkolai* Rich et al., 1978) and may be antecedent to the entire zygomaticine radiation (Black & Archer, 1997a). Four species of *Neohelos* are recognised (P. Murray pers. comm.). *Neohelos* sp. nov. 1, a small plesiomorphic form; *N. tirarensis* a medium-sized moderately derived form from the Kutjamarpu Local Fauna, South Australia; *Neohelos* sp. nov. 2, a large derived form from the Bullock Creek Local Fauna, NT, antecedent to *Kolopsis torus* (Woodburne, 1967) of the late Miocene Alcoota Local Fauna, NT; and *Neohelos* sp. nov. 3, a highly derived form structurally

	SYSTEM A										SYSTEM B							SYSTEM C										PL	
	D	B	H	B	S	J	V	A	W	W	C	N	D	M	I	H	R	L	G	D	J	H	J	90	J	D	C	E	T
LOCAL FAUNAS ♦	O			R	B	A	P	L	H	W	S	G	T	M	N	T				I	S	H	J		C	S	O	N	E
<i>S. michaelbirti</i>			1																										
<i>S. johnnilandi</i>							2																						
<i>Silvabestius</i> sp.	1																									10			
<i>Neohelos</i> sp. nov. 1	1	1		1	1																								
<i>N. tirarensis</i>	1			1						1	1	1		1	1						1								
<i>Neohelos</i> sp. nov. 2																		1				4							
<i>Neohelos</i> sp. nov. 3																							2						
<i>Ni. lavarackorum</i>																	1	1	1					24	1	2			
<i>Nimbadon</i> sp.																							1						
Zygomaturine gen. nov.													2																
<i>B. angulatum</i>	1	1	2		4	1			3																				
<i>Bematherium</i> sp.								1																					
<i>Ngapakaldia</i> sp.					1																								
<i>Pr. ponticulus</i>	1			1	2	1				1	1	1						1											
<i>Pr. novacula cephalus</i>																					1	1							
<i>Palorchestes anulus</i>																												1	
<i>P. azael</i>																													1
<i>Diprotodon optatum</i>																													1
TOTAL	5	2	2	3	4	2	1	1	1	2	2	2	1	1	1	1	3	1	2	2	1	2	1	1	1	1	1	2	

FIG. 1. The distribution of diprotodontoid taxa through the Riversleigh sequence. Numbers indicate the minimum number of individuals for each species found in a given local fauna. PLEI=Pleistocene. System B heading is subdivided into: L=Low, MID=Middle and H=High Local Fauna Abbreviations: AL, Alsie; 90, Alan's Ledge 1990; BO, Burnt Offering; BR, Bone Reef; CO, Cleft of Ages (tentatively regarded as System C); CS, Camel Sputum; D, D-Site; DI, Diprotodont Site; DS, Dome Site; DT, Dirk's Towers; EN, Encore Site; G, Gag Site; H, Hiatus Site; HH, Henk's Hollow; IN, Inabeyance; JA, Jeanette's Amphitheatre; JC, Jim's Carousel; JJ, Jaw Junction; JJS, Jim's Jaw Site; MM, Mike's Menagerie; NG, Neville's Garden; RT, Ringtail Site; SB, Sticky Beak Site; TE, Terrace Site; WH, White Hunter; VIP, VIP Site; WW, Wayne's Wok.

transitional between *Neohelos* sp. nov. 2 and *Kolopsis yperus* (Murray et al, 1993) from the late Miocene Ongeva Local Fauna, Waite Formation. *Bematherium* sp. is known from a single maxillary fragment which is plesiomorphic relative to *B. angulum*. A new unnamed species of *Ngapakaldia* is more derived than the central Australian *N. tedfordi* but plesiomorphic relative to *N. bonythoni*. Fragmentary material of Zygomaturine gen. nov. has an uncertain phylogenetic position. *Nimbadon* sp. is similar to *N. lavarackorum* in size, molar morphology and cranial profile; however, differences in upper premolar morphology may imply a more plesiomorphic position within the genus. However, I doubt whether this single skull is indicative of a new species. Extreme intraspecific variation in P<sup>3</sup> morphology is common among Tertiary zygomaturines (e.g. *Neohelos* spp.; P.

Murray pers. comm.) with reduction or loss of premolar cusps a relatively common phenomenon. Comparable cranial material for *Ni. lavarackorum* has yet to be processed. *Propalorchestes ponticulus* (Murray, 1990b) is plesiomorphic relative to *P. novaculacephalus*. *Propalorchestes novaculacephalus* occurs in the Bullock Creek Local Fauna; Murray (1990b) indicated that this material is more derived than the Riversleigh specimens. *Palorchestes anulus* is intermediate between *Pr. novaculacephalus* and *Palorchestes painei* from the late Miocene Alcoota Local Fauna (Black, 1997). *Palorchestes azael* and *Diprotodon optatum*, the most derived members of Palorchestidae and Diprotodontidae, respectively, are known from Terrace Site, which has been radiocarbon dated at approximately 23,900±4,100-2,700 years BP (Davis & Archer, 1997).

## DISCUSSION

**AGREEMENT WITH PROPOSED STRATIGRAPHY.** The distribution of diprotodontoids throughout the Riversleigh systems is generally consistent with Archer et al.'s (1989, 1994a, 1995) proposed stratigraphic framework. The most plesiomorphic forms are restricted to the older System A local faunas, and more derived taxa become more abundant in Systems B and C.

A similar pattern of distribution is evident within lineages. There is a gradual evolution in cranial and dental morphology accompanied by an increase in body size within *Neohelos* and *Propalorchestes*, respectively, through the Riversleigh sequence (Murray, 1990b; pers. comm.). Although some temporal overlap is evident, generally *Neohelos* sp. nov. 1 is the dominant form in System A. *N. tirarensis* is most abundant in System B, *Neohelos* sp. nov. 2 spans low to high System C and *Neohelos* sp. nov. 3 is unique to high System C Jaw Junction Site.

A similar succession is exhibited by palorchestids. Plesiomorphic *Propalorchestes ponticulus* is relatively common in System A and B Sites, and is succeeded by the more derived *Pr. novaculacephalus* in mid-high System C Sites.

**INTRACONTINENTAL COMPARISONS.** The Riversleigh assemblages contain the most diverse array of diprotodontids and palorchestids of any single region on the continent. Of the 9 genera, *Neohelos*, *Nimbadon*, *Ngapakaldia*, *Propalorchestes* and *Palorchestes* are also known from the Oligocene-Miocene in central and northern Australia. The biochronological potential of some of these genera is, however, limited, because of uncertainty about interspecific affinities. *Neohelos*, *Propalorchestes* and *Palorchestes*, are biochronologically most significant.

*Neohelos tirarensis* from System B is close to the type material from the Kutjamarpu Local Fauna suggesting age equivalence; this is supported by other shared taxa such as *Wakiewakie lawsoni* (Godthelp et al., 1989), *Paljara* (Archer, 1994), *Wakaleo oldfieldi* (A. Gillespie pers. comm.), *Namtilanadeta*; *Nambaroo* (Archer et al., 1989) and *Litokoala* (Black & Archer, 1997b).

*Neohelos* sp. nov. 1 in Systems A-C is more plesiomorphic than *N. tirarensis* suggesting that some of Riversleigh's stratigraphic units predate the Kutjamarpu Local Fauna. *Neohelos* from faunal zones D-E of the Etadunna Formation have not been specifically identified (Woodburne et

al., 1993). Murray (pers. comm.) suggests that if this material is found to represent *tirarensis* then some of Riversleigh's older deposits may predate mammal-bearing Etadunna Formation.

Myers & Archer (1997) correlated White Hunter Site (System A) and Mammalon Hill (Zone D, Etadunna Formation), the latter 24.7-25 MY BP (Woodburne et al., 1993).

?*Ngapakaldia* sp. nov. in System A extends the generic distribution from South Australia. This species appears to be more derived than *N. tedfordi* from the Ngapakaldi and Ngama Local Faunas (Etadunna Fmn) and the Tarkarooloo Local Fauna (Namha Fmn), yet plesiomorphic relative to *N. bonythoni* from the Ngapakaldi Local Fauna. *Ngapakaldia* also occurs in faunal zones C, D and E of the Etadunna Fmn. As with *Neohelos*, species level identification is necessary before *Ngapakaldia* will be of use in biostratigraphy.

*Propalorchestes novaculacephalus* and *Neohelos* sp. nov. 2 in low to mid System C assemblages confirms previous hypotheses (Archer et al., 1989; 1994a; 1995) that they are of a similar age to the Bullock Creek Local Fauna (Fig. 2). Correlation is further supported by the shared *Nimbacinius dicksoni* (Muirhead & Archer, 1990), *Wakaleo vanderleuri* (Murray & Megirian, 1990) and *Balbaroo* sp. (Flannery et al., 1983).

*Neohelos* sp. nov. 3, the largest and most derived species of *Neohelos*, occurs in the Jaw Junction assemblage suggesting that this high System C deposit is younger than the Bullock Creek Local Fauna. *Neohelos* sp. nov. 3 exhibits an upper third premolar morphology that anticipates the condition found in the more derived zygomatic *Kolopsis*, which first appears in the Alcoota and Ongeva Local Faunas of the Waite Fmn, Northern Territory. Ancestor-descendent relationships are well supported for the *Neohelos/Kolopsis/Zygomaticus* clade (Stirton et al., 1967; Murray et al., 1993). The presence of *Neohelos* material, structurally transitional between Bullock Creek's *N.* sp. nov. 2 and the Waite Formation's *Kolopsis* further suggests this correlation making some of Riversleigh's high System C deposits, such as Jaw Junction Site, younger than the Bullock Creek Local Fauna but older than late Miocene deposits of the Waite Formation.

This is also true of Riversleigh's Encore assemblage which, on the basis of its derived and often unique fauna, is believed to be early late Miocene in age (Archer et al., 1995). This is based on the

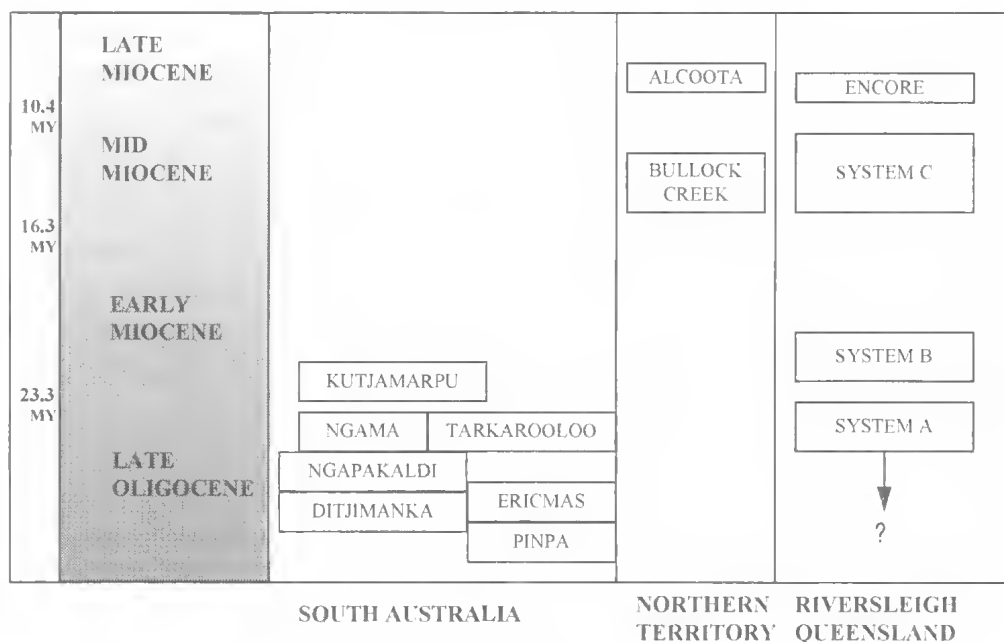


Fig. 2. Tentative correlation of Riversleigh's Oligo-Miocene fossil deposits with the Etadunna and Wipajiri Formations, South Australia and the Alcoota and Bullock Creek local faunas, Northern Territory based on diprotodontoid stage-of-evolution comparisons.

presence of several taxa which exhibit adaptations to the onset of drier climates during the late Miocene as well as taxa whose lineages extend into Pliocene and Pleistocene times. These include: *Palorchestes anulus* which is structurally antecedent to *P. painei* from the late Miocene Alcoota Local Fauna (Black, 1997); a small *Phascolarctos*; a hyselodont vombatid related to the late Cainozoic *Warendja wakefieldi* (Archer et al., 1995); a thylacoleonid intermediate between *Wakaleo vanderleuri* and the late Miocene *Wakaleo alcootense* (A. Gillespie pers. comm.); a giant rat kangaroo, *Ekaltadeta janiemulvaneii* (Wroe, 1996), which is possibly antecedent to Pleistocene *Propleopus*; and *Mayigriphus orbus* (Wroe, 1997), a dasyuromorphian with some features correlated with drier environments in modern dasyurids.

**DIVERSITY AND FAUNAL CHANGE.** System A sites contain the highest number of contemporaneous diprotodontoids with 5 species at Site D and 4 at Sticky Beak Site (Figs 1-2). A drop in diversity is evident in System B with only 1 or 2 species per site. Diversity increases slightly in low to middle System C assemblages with generally 1-2 contemporaneous diprotodontoid spe-

cies. Conversely, upper System C deposits exhibit a decline in diprotodontoid diversity. If we consider the small number of taxa being analysed such changes in diprotodontoid diversity may not be significant. However, a similar decline in both family- and generic-level diversity is evident in a number of other marsupial groups during the middle to late Miocene. This decline may be related to the late Miocene onset of 'icehouse' climatic conditions resulting in the regional collapse of rainforest and subsequent spread of open forest and woodland/savanna (Archer et al., 1994b; 1995).

Replacement of rainforest habitat by more open forest may have benefited select diprotodontoids which is reflected in an increase in species abundance for some System C Local Faunas. Relatively high 'minimum number of individuals' estimates for species of *Nimbadon* and *Neohelos* sp. nov. 1 have been recorded from AL90 and Cleft of Ages Sites respectively. This may suggest that individuals of these species were roaming in mobs, a feature characteristic of slow moving medium- to large-sized herbivores in relatively open environments.

It is also feasible that high abundance in the above System C assemblages, and conversely low



abundance in System A-B assemblages, may represent sampling or taphonomic biases. Likewise, the absence of diprotodontines in System B and C may be an artefact of incorrect taxonomic assignment. Even so, several zygomatic species recovered from System B and System C assemblages appear to have developed a number of diprotodontine-like features of their dentition. These include the reduction of the parastyle and loss of the hypocone on  $P^3$  and a reduced paraeristid on  $M_1$ . A similar phenomenon has occurred in the Alcoota Local Fauna where dental and cranial morphology of the zygomatic *Alkwertatherium webbi* is convergent on that of the diprotodontine *Pyramios alcootense* (Murray, 1990a). In general, zygomatics display a higher diversity and abundance in Tertiary fossil assemblages than diprotodontines. This may reflect their greater ability to adapt to changing environments than their diprotodontine counterparts. It is further reflected in Riversleigh's System B and System C Local Faunas, where diversifying zygomatics have subsequently radiated into vacant niches occupied by diprotodontines during the late Oligocene.

Diprotodontoids are not known from Riversleigh's Pliocene assemblages. They seem to have declined markedly in generic diversity throughout the Australian Pliocene. Significant faunal turnover is characteristic of most marsupial families during the late Miocene and early Pliocene (Archer et al., 1995).

The drop in diversity of diprotodontid and palorchestid species continues into the Pleistocene, with only one member of each family represented (Fig. 1). Both species are common throughout Australia's Quaternary fossil deposits, yet both are the last of their respective lineages. This decline in diprotodontoid diversity may be a consequence of unsuccessful competition with rapidly diversifying mesic and xeric macropodoids (Archer et al., 1994).

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